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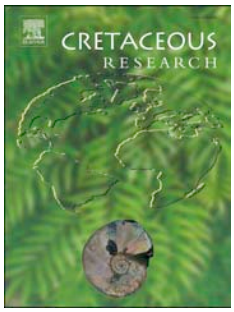

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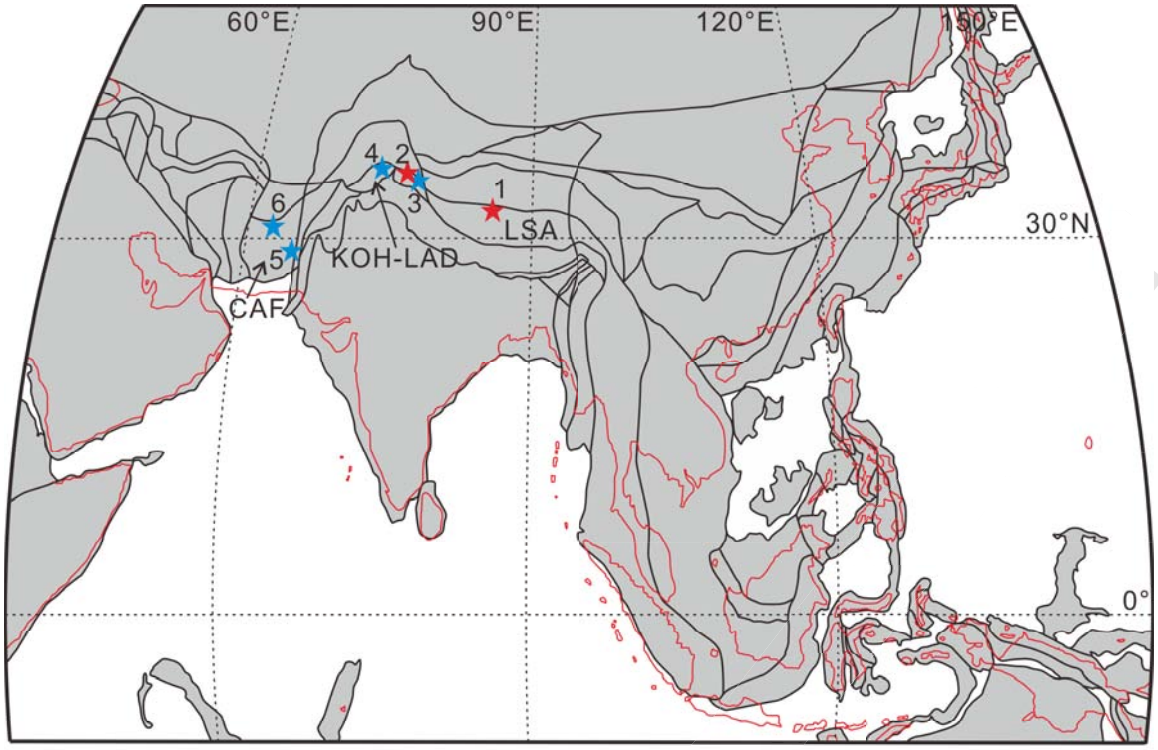
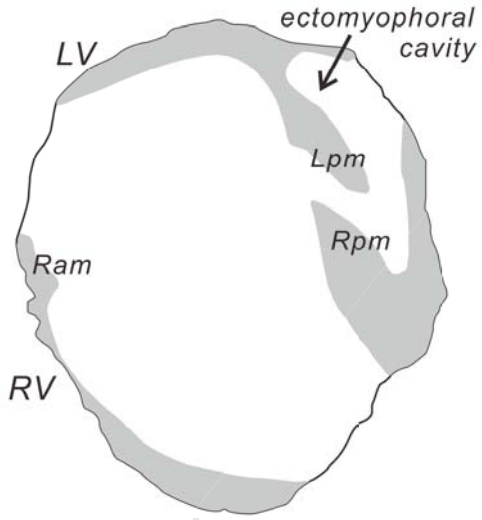
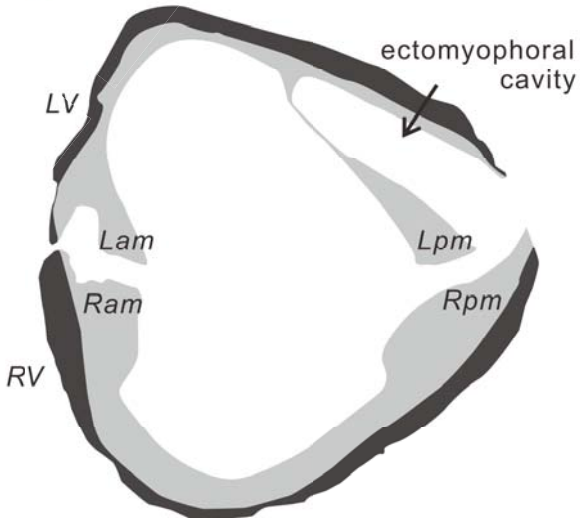


★ ***Horiopleura haydeni***



★ ***Shajia tibetica* gen. et sp. nov.**



Shajia, a new genus of polyconitid rudist from the Langshan Formation of the Lhasa Block, Tibet, and its palaeogeographical implications

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Abstract.

A new polyconitid rudist *Shajia tibetica* gen. et sp. nov., of late Aptian to Albian age, is described from the Langshan Formation of Nyima County, northern Lhasa Block, Tibet. Though comparable in size and external morphology with *Horiopleura haydeni* Douvillé, which is a common endemic species in southwestern Asia, *Shajia* differs from the latter species in its possession of an inwardly inclined, instead of outwardly facing, posterior myophore in the right valve. In addition, a single specimen from Ladakh, which was previously assigned to *Polyconites*? sp., on account of a similar myophoral distinction from *H. haydeni*, is transferred to the new genus. *Shajia* is considered most likely to have been derived from one of a group of *Horiopleura* species that lived on the southern margin of the Mediterranean Tethys.

The so-called 'Yasin fauna' represented by the late Aptian to Albian *Horiopleura haydeni*/*Auroradiolites gilgitensis* rudist association, is considered to be restricted to southwestern Asia, including Afghanistan, Kohistan in northern Pakistan and Ladakh in northern India, though those two species in particular have not so far been recorded from the Lhasa Block of Tibet. Nevertheless, *S. tibetica* co-occurs with *Auroradiolites biconvexus* (Yang et al.), which probably evolved directly from *A. gilgitensis* (Douvillé), and the age of the latter association is in accordance with the generally

accepted age of the Yasin fauna as late Aptian to Albian. Hence the *S. tibetica* and *A. biconvexus* association can be considered a regional variant of the Yasin fauna, which had evidently already dispersed to the Lhasa Block by the late Aptian. So the Langshan Formation can be considered palaeogeographically linked with other mid-Cretaceous shallow-marine carbonate deposits in adjacent southwestern Asian regions. These findings also provide new evidence that the age of the rudist assemblage of the Lhasa Block is late Aptian to Albian, although a slightly younger age cannot be excluded.

Keywords: Lhasa Block; Langshan Formation; mid-Cretaceous; Rudists; Polyconitidae; Yasin fauna

1. Introduction

Rudists are an extinct order of bivalves that flourished on the carbonate platforms of the Tethyan–Atlantic–Pacific oceanic realm during the Late Jurassic to Cretaceous (Skelton, 2018). The mid-Cretaceous rudists of southwestern Asia and the western Pacific region show great similarity and affinity (Sano and Masse, 2013; Skelton et al., 2013). Accordingly, the Southwest Asian/Pacific Faunal Province was proposed, covering Iran, Afghanistan, Kohistan in northern Pakistan, Ladakh in northern India, Tibet in China and Japan, as well as Cebu Island and the Japanese seamounts in the Pacific region (Rao et al., 2015, 2017). The rudist fauna of this province is dominated by the endemic radiolitid *Auroradiolites* Rao et al., 2015 and the polyconitid lineage of *Horiopleura haydeni* Douvillé, 1926–*Praecaprotina* Yabe

and Nagao, 1926– *Magallanesia* Sano et al., 2014, as well as some more widely dispersed taxa such as *Eoradiolites* Douvillé, 1909 and *Sellaea* Di Stefano, 1889 (Skelton et al., 2013; Sano et al., 2014; Rao et al., 2015). The orbitolinid assemblage associated with these rudists is likewise composed of several endemic taxa such as *Mesorbitolina birmanica* (Sahni, 1937), *Palorbitolinoides orbiculata* Zhang, 1986 and *Palorbitolinoides hedini* Zhang, 1986, together with cosmopolitan taxa such as *Mesorbitolina texana* (Roemer, 1849), *M. subconcava* (Leymerie,1878) and *M. aperta* (Erman, 1854) (Cherchi and Schroeder, 2013; Schlagintweit and Wilmsen, 2014; Rao et al., 2015, 2017; Boudagher–Fadel et al., 2017).

Within the SW Asian/Pacific Faunal Province, the so-called 'Yasin fauna' of rudists represented by the late Aptian–Albian *Horiopleura haydeni*/*Auroradiolites gilgitensis* association had a widespread distribution in southwest Asia including Iran, Afghanistan, Kohistan, and Ladakh (Douvillé, 1926; Rossi Ronchetti, 1965; Montenat et al., 1982; Upadhyay, 2001, 2014; Skelton et al., 2005; Sha and Cestari, 2016). In the mid-Cretaceous, these fossil sites were all located on blocks/terranes arrayed along, or offshore from the southern Asian margin on the northern side of the eastern Neo-Tethyan Ocean (Rao et al., 2017). The Yasin fauna, as such, has not previously been recorded from the Lhasa Block, which occupied a similar geographical and tectonic position to the blocks/terranes mentioned above. Instead, *Auroradiolites biconvexus*, probably derived directly from *A. gilgitensis*, and the canaliculate polyconitid genus *Magallanesia* were found there (Rao et al., 2015; 2017).

In this study, a new polyconitid genus, *Shajia*, which is superficially comparable

with *Horiopleura haydeni*, is described, based on articulated specimens collected from the Langshan Formation of Nyima County, Lhasa Block. A single specimen collected in Ladakh and formerly assigned to *Polyconites*? sp., by Masse and Fenerci-Masse (2017) is also reappraised in the light of the new material from the Lhasa Block. The relationship of *Shajia* with the Yasin fauna and its palaeogeographical implications are evaluated and the age of the rudist fauna from the Langshan Formation revised accordingly.

2. Geological setting

The Qinghai–Tibet plateau is generally regarded as a complex tectonic collage of several blocks; from north to south they are the Songpan–Ganze–Hoh Xil, Qiangtang, Lhasa and Tethyan–Himalayan blocks, which are separated from each other by sutures (Yin and Harrison, 2000; Zhu et al., 2013). These blocks rifted from Gondwana, drifted northward, and finally accreted to the Asian continent successively during the late Palaeozoic and Mesozoic eras, prior to the India–Asia collision (Pan et al., 2012; Li et al., 2017). Today, the Lhasa Block is bounded by the Bangong–Nu suture to the north and the Indua–Yarlung suture to the south (Fig. 1A; Yang et al., 2015). It rifted from the India–Gondwana continent in the Late Triassic, and collided with Asia in latest Jurassic–earliest Cretaceous times (Yin and Harrison, 2000; Metcalfe, 2006).

[Figure 1 hereabouts]

In the late Early to early Late Cretaceous (Barremian–Cenomanian), the Lhasa

Block had already collided with the Qiangtang Block, and was located on the north side of the eastern Tethys Ocean. At this time, shallow marine carbonate deposits, represented by the Langshan Formation, were widely distributed along the northern portion of this block (Leier et al., 2007; Rao et al., 2015). The Langshan Formation crops out as a nearly east-west-oriented belt extending from Baingoin County in the east to Rutog County in the west (XZBGM, 1993). It is dominated by dark-grey to black limestone sometimes interbedded with siltstone and mudstone (Zhang et al., 2004; Leier et al., 2007). The thickness of the Langshan Formation is poorly constrained and has considerable lateral variation; in this paper, we regard it as about 1000 m, referring to Zhang et al. (1986), Leeder et al. (1988), and Leier et al. (2007).

Abundant fossils have been recorded from the Langshan Formation, dominated by orbitolinids (Zhang, 1982, 1986, 1991; Boudagher–Fadel et al., 2017), rudists (Yang et al., 1982; Gou and Shi, 1998, Scott et al., 2010; Rao et al., 2015, 2017), gastropods (Yu and Xia, 1985) and corals (Löser and Liao, 2001; Deng and Wang, 2013). The age of the Langshan Formation is mainly constrained by foraminifers, especially large benthic orbitolinids. Deposition started from the Early Barremian based on the occurrence of *Eopalorbitolina charollaisi* Schroeder and Conrad, 1968 (Rao et al., 2015), and extended to the Early Cenomanian, as indicated by the appearance of *Daxia cenomana* Cuvillier and Szakall, 1949, *Nezzazata conica* (Smout, 1956), *Cuneolina* cf. *cylindrica*, *Orbitolina qatarica* Henson, 1948, *Conicorbitolina* sp. A and *Pseudedomia* sp. (Boudagher–Fadel et al., 2017).

The polyconitid specimens described herein were collected from the Langshan

Formation on the western side of Dangqiong Lake in southern Nyima County (Fig. 1B). This fossil site is located in the southern Nyima Basin, about 450 km northwest of Lhasa (DeCelles et al., 2007; Kapp et al., 2007). No palaeontological data have previously been published from the Langshan Formation of the Nyima Basin. According to the observations of Tong Zhang and Zhaoxiong Ma during field work, these specimens were collected from the lower part of the upper Langshan Formation. Furthermore, several large specimens of *Auroradiolites* were collected from the same bed as these polyconitid specimens. Although the left valves of these *Auroradiolites* specimens were not preserved, they are most likely attributable to *A. biconvexus* because of the large size of the right valves. As the age range of *A. biconvexus* was revised to late Aptian–Albian (Rao et al., 2017), and the geological range of the upper Langshan Formation is late Aptian to early Cenomanian (Rao et al., 2015), a late Aptian to Albian age can be assumed for these polyconitid specimens.

3. Systematic palaeontology

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://www.zoobank.org/References/xxxxxx

The numbered specimens are housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China (NIGPAS).

Abbreviations: *at*, anterior tooth; *ct*, central tooth; *Lam*, anterior myophore of left valve; *Lig*, Ligamentary infolding; *Lpm*, posterior myophore of left valve; *LV*, left valve; *ol*, outer shell layer; *pt*, posterior tooth; *Ram*, anterior myophore of right valve;

Rpm, posterior myophore of right valve; *RV*, right valve.

Quantitative characters (Fig. 2): *Dap*, antero–posterior commissural diameter, *Ddv*, dorso–ventral commissural diameter; *Hd*, dorsal height of *RV*; *Hv*, ventral height of *RV*; *LVc*, convexity of the *LV*.

The suprageneric classification used herein follows Skelton (2013*a, b*).

[Figure 2 hereabouts]

Order HIPPURITIDA Newell, 1965 (*nom. correct*. Scarlato & Starobogatov, 1971, *pro* Order Hippuritoida Newell, 1965; emend. Bouchet *et al*. 2010)

Suborder HIPPURITIDINA Newell, 1965 (Skelton, 2013b)

Superfamily RADIOLITOIDEA d'Orbigny, 1847

Family POLYCONITIDAE Mac Gillavry, 1937

Genus SHAJIA gen. nov.

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***Type species*.** *Shajia tibetica* gen. et sp. nov.

***Derivation of name*.** The new genus is named for Professor Jingeng Sha, a well-known Chinese palaeontologist who has made extensive studies of Mesozoic bivalves and of the geological evolution of the Qinghai–Xizang Plateau (Tibet). In recent years, he has focused on reviewing the rudist record of China, including publication of an important paper in *Cretaceous Research* to revise the late Aptian–Albian Yasin-type rudist fauna of the Himalayan area (Sha and Cestari, 2016). We chose his name as the root for the new genus erected herein in honour of his

contributions to Himalayan, and especially Tibetan rudist research.

Diagnosis. Large-sized polyconitid (antero-posterior commissural diameter can reach 90mm). *RV* conical and slightly twisted, *LV* low capuloid with dorsally over-hanging umbo. Ventral height of *RV* is less than twice the dorsal height, resulting in a dorsally inclined commissure. Outer shell layer is relatively thick, especially in the *RV* where its thickness may reach nearly 10 mm, on which longitudinal ribs are also developed. Subequal teeth of *LV* (*at* > *pt*) straddling the straight and erect central tooth of *RV*. Ligamentary infolding strongly developed. *LV* anterior myophore a narrow, flat-ended buttress projecting in from the anterior valve wall and facing onto the shelf-like anterior myophore of the *RV*, which is formed by a thickening of the inner shell layer. Posterior myophore in *LV* is a plate projected subparallel to the posterior valve wall, from which it is thus separated by a sub-rectangular ectomyophoral cavity; the adductor insertion surface on the broad tip of the *Lpm* is inclined somewhat outwards so as to face onto the depressed, inwardly sloping surface of the *RV* posterior myophore, which is formed by a pillow-like swelling of the inner shell layer.

[Figure 3 hereabouts]

Discussion. The thickening of the outer shell layer, especially of the *RV*, the subequal teeth of the *LV* (*at* > *pt*) and reflexed plate-like *Lpm* with adjacent ectomyophoral cavity, all observed in the Nyima specimens (Figs. 3A; 4-6) are diagnostic characters of the family Polyconitidae Mac Gillavry, 1937 (Skelton, 2013a). Comparisons thus need to be made with the handful of known genera in that family, starting with those

most easily excluded from further consideration.

The lack of sub-division into multiple canals of the *LV* posterior ectomyophoral cavity of the Nyima specimens (Figs. 3A) rules out the genus *Magallanesia* Sano et al., 2014 (= 'Polyconitid new taxon 1' in Skelton et al., 2013) (Fig. 3F). The genus *Polyconites* Roulland, 1830, can also be excluded as the *LV* of this genus is nearly flat (operculiform), the external surface of the shell lacks ribbing, and the posterior myophore of the *RV* is generally represented only by a slight thickening of the inner shell layer, at least in more derived species (Fig. 3D) (Masse et al., 1998; Skelton and Masse, 1998; Skelton, 2013a), although it is a little more prominent in juvenile shells of more primitive species (Skelton et al., 2010).

The external morphology of the Nyima specimens is similar to that of the genus *Horiopleura*, including the sparse, subdued longitudinal ribs (Fig. 4D), similar to those described from the Himalayan species *Horiopleura haydeni* by Douvillé (1926) and Rossi Ronchetti (1965). Moreover, the anterior myophoral arrangement of *Shajia* differs little from that seen in *Horiopleura* species (e.g., Fig. 3C). However, the depressed, inwardly sloping *Rpm* in the Nyima specimens (Fig. 3A) contrasts sharply with that in *Horiopleura haydeni*, which projects upward so as to face back onto the inner face of the *Lpm* (Fig. 3B). The same contrast is observed, moreover, in the type species of *Horiopleura*, *H. lamberti* Douvillé, 1889 (Fig. 3C), as well as in the more derived genera *Praecaprotina* (Fig. 3E), and 'Polyconitid new taxa 2 and 3' (Skelton et al., 2013), both of the latter additionally showing only a weakly convex LV.

Otherwise, both *Tepeyacia* and 'Polyconitid new taxon 4' (Skelton et al., 2013) are characterized by distinctive pleated infoldings of the *RV* outer shell layer, not observed in the Nyima specimens, while the polyconitid affinity of *Douvillelia* and *Jerjesia* is in any case questionable (Skelton, 2013a; Masse et al., 2015) as neither appears to possess the diagnostic *LV* posterior ectomyophoral cavity.

In a recent review of the genus *Horiopleura*, however, Masse and Fenerci-Masse (2017, p. 54) noted that the outwardly inclined (facing towards the posterior side) and/or concave upward form of the *Rpm* (as in Fig. 3B, C) is 'reported in the group of large, advanced species, e.g. *Horiopleura lamberti*; [whereas] in the group of small, putative primitive species, the inclination may be inwards (towards the anterior side), but a posterior shoulder is always present, a character that differentiates it from *Polyconites'*. All the figured specimens of the 'putative primitive species' assigned to *Horiopleura* by Masse and Fenerci-Masse (2017; e.g., Figs. 7C, 8E, F, 9A, B, 13A3 therein) indeed show this 'shoulder' to be a consistent attribute, such that adductor insertion area on the *Rpm* invariably forms a distinct ledge (either flat or slightly concave) that is oriented sub–parallel to the commissural plane.

Nevertheless, an Albian specimen from Parnassus, Greece, described by Masse and Fenerci-Masse (2017; Fig. 19B therein) and assigned by them to *H. distefanoi* Parona, 1909, does show an inwardly sloping *Rpm* with a correspondingly suppressed internal shoulder – a feature accordingly incorporated in their diagnosis for the species: 'RV ledge like posterior myophore sloping inwards' (Masse and Fenerci-Masse, 2017; p.

72). Accordingly, we suggest that the species that includes that specimen, if not *H. distefanoi* itself (pending confirmation the myophoral condition cited above in that species), might be allied with the new genus proposed herein, as an intermediate form, on the grounds that it differs from other species of *Horiopleura* by the marked inward inclination of the *Rpm* with associated suppression of the internal shoulder. This myophoral distinction is analogous to that which was used diagnostically to separate the earliest species of *Polyconites*, *P. hadriani*, from its inferred ancestral species of *Horiopleura* (Skelton et al., 2010), though additionally accompanied in that case by the pronounced flattening of the LV, in contrast to *Shajia*. Likewise, we propose that a single specimen from Ladakh that was assigned to *Polyconites*? sp., by Masse and Fenerci-Masse (2017), and which shows remarkably similar characteristics to those of the Nyima specimens (see below), should also be transferred to the genus *Shajia*.

Age and distribution. Late Aptian to Albian for the rudist-bearing limestone bed of Nyima County in Tibet (China), and late Aptian for the single specimen recorded from Ladakh (northern India); therefore, a late Aptian to Albian age should be assigned to this new genus based on current records.

Shajia tibetica sp. nov.

Figures 4–6

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? aff. 2017 *Horiopleura distefanoi* (Parona, 1909) Masse and Fenerci-Masse, fig. 19B

2017 *Polyconites* ? sp. Masse and Fenerci-Masse, fig. 20

Derivation of name. From Tibet, the type locality where the new species was found.

Material. Two articulated specimens (NIGP. 110522-110523), with the outer shell layer partially worn. The *RV* apices of both specimens were broken.

Holotype. Articulated specimen (NIGP. 110522; Figs. 4, 5). Two antero-posterior sections cutting through both valves were made (Fig. 4C), the more ventral section (Fig. 5A-B) oblique to the commissural plane and the more dorsal section (Fig. 5C-D) sub-perpendicular to it.

Paratype. Articulated specimen (NIGP. 110523; Fig. 6). Three obliquely transverse sections were made (Fig. 6A): the upper one cuts through both valves (the over-hanging dorsal part of the *LV* and the ventral part of the *RV*, Fig. 6C); the middle one cuts mainly across the *RV*, though including the umbonal tip of the *LV* (Fig. 6D, E); and the lower section cuts across the *RV* only (Fig. 6F).

Localities. The specimens were collected from the Langshan Formation of Nyima County, Tibet. The fossil site is located at the west side of Dangqiong Lake (E 86°27′23″, N 31°36′53″; Fig. 1B).

Diagnosis. As for genus.

[Figures 4–6 hereabouts]

Description.

***External morphology*.** The two specimens are relatively large; although both *RV* apices are broken, values of *Hd* can be estimated at about 70 mm, and of *Hv* up to 120 mm, creating a dorsally inclined commissure. The *RV* is slightly twisted and curved and the *LV* is of low capuloid form, becoming gradually lower from the dorsal to ventral parts (Fig. 4C). The commissure is sub-rounded in the holotype, with a 90 mm diameter, whereas in the paratype it is elliptical because of dorso-ventral compression, with a 90 mm *Dap* and a 50 mm *Ddv*. Although the *ol* is partly worn or encrusted, blunt longitudinal ribs could be observed in each *RV* (Figs. 4D, 6B); rib width is about 2 mm. In the *LV*, fine costae radiate from the apex to the commissural rim.

The invaginated ligament, supported on an infolding of the dark outer shell layer, created a longitudinal furrow on the dorsal flank of the *RV* (Fig. 6A, F). The extent of external wear of the specimens precludes the possibility of recognizing radial bands either in the transverse sections, or on the natural surfaces of the shells.

***Internal organization*.** The thickness of the dark outer shell layer may approach 10 mm in parts of the *RV* (Figs. 5, 6C-F). In the *LV*, in contrast, it is only a few mm thick, thickening slightly towards the commissure (Fig. 5). The inner shell layer is thick, especially in the myocardinal area, and has been replaced by white to pale grey calcite spar (Figs. 5, 6 C, D, F). In the oblique transverse section of the paratype *RV*, the *ol* infolding associated with the invaginated ligament is about 3 mm wide and 6 mm in length, and a small ligamentary cavity wraps around its truncated inner tip (Fig. 6F).

The myocardinal complex is well displayed in both specimens despite some localized boring and minor disruption by narrow, spar-filled fractures and stylolites.

The *Lpm* is prominent, pedunculate, and reflexed so as to lie nearly parallel to the over-arching posterior shell wall of the *LV*, from which it is thus separated by an ectomyophoral cavity of sub-rectangular shape in section (Fig. 5C, D); a narrow annexe extends dorsally from the latter cavity above the *pt* (Figs. 5A, 6C, '*o*'). The tip of the *Lpm*, where the adductor muscle attached, faces outwards onto the depressed and inwardly sloping face of the *Rpm*, which is formed by a swelling of the *RV* inner shell layer (Fig. 5C, D). The *Rpm* thus appears in transverse section simply as a solid thickening of the posterior inner shell, lacking any indication of an ectomyophoral cavity behind it (Fig. 6D-F). The *Lam* is a protruding buttress with a bluntly sub-rectangular termination in section, separated from the anterior valve wall by a narrow gutter (Figure 5D). Its counterpart in the *RV*, the *Ram*, is formed by a shelf-like thickening of the inner shell layer (Figs. 5C, D, 6D-F). The *ct* in the *RV* is an erect, robust ridge interposed between the *at* and *pt* of the *LV* (Fig. 5A; 6D, E); *at* is slightly larger than *pt* (Fig. 6D-F).

***Remarks*.** The single Ladakh specimen, which was assigned to *Polyconites* ? sp., by Masse and Fenerci-Masse (2017; Fig. 20 therein), is closely comparable with the Nyima specimens. It is similar to them in terms of the external morphology of the shell (including the low capuloid form of the *LV*), the longitudinal ribbing of the *RV*, and the myocardinal apparatus, with, in particular, a depressed, inward-sloping *Rpm* lacking a prominent internal shoulder (hence the appearance of 'strong affinity with *Polyconites'* noted by Masse and Fenerci-Masse, 2017, p. 72). Though somewhat smaller than the Nyima specimens, this specimen is virtually identical in form to the

type material found in Tibet and can thus be considered conspecific.

As noted earlier, in the discussion of the genus, the specimen assigned to *Horiopleura distefanoi* by Masse and Fenerci-Masse (2017) and thus perhaps that species – of similar age to *Shajia* – likewise shows a comparable myophoral configuration, as well as a *LV* of low capuloid shape. Taken together with other associated forms discussed by them, such similarities may bear upon the evolutionary origin of the new genus.

Age and distribution. As for genus.

4. Discussion

4.1 Phylogenetic relationship of *Shajia* to other polyconitids

At first sight, *Shajia* appears to have a chimaeric combination of characters from both *Horiopleura* and *Polyconites*: while its external shell form and ornamentation are very similar to those of the larger species of *Horiopleura*, the posterior myophoral arrangement, in particular, approaches that of *Polyconites*. Notwithstanding its distinction from both of those genera, derivation from either of them appears plausible: i.e., either from *Horiopleura*, through progressive inward inclination and depression of the *Rpm*, analogously to that proposed for the earlier origination of *P. hadriani* from an older *Horiopleura* sp. (Skelton et al., 2010), though without flattening of the *LV* and loss of ribbing; or, alternatively, from a *Polyconites* sp., through reversal of the *LV* flattening, to re–acquire a *Horiopleura*–like external shell shape, meanwhile retaining a depressed, inwardly–inclined *Rpm* – in contrast to the pronounced posteriorward tilt of the *Rpm* in the more derived species of *Horiopleura*.

Although *Shajia* is externally quite similar to the co-eval SW Asian *H. haydeni* in size, morphology, longitudinal ribs on the *RV*, as well as with respect to dentition, on the evidence of the few specimens known so far, it differs sharply from the latter species in its posterior myophoral organisation. Specifically, 1) the *Lpm* of *Shajia* is strongly reflexed posteriorly, such that it is nearly parallel to the posterior *LV* shell wall, forming a narrow sub-rectangular ectomyophoral cavity between them, whereas in *H. haydeni*, the *Lpm* protrudes more directly down into the *RV*; 2) correspondingly, the *Rpm* of *Shajia* is formed by the low, inward-facing swelling on the inner shell layer, whereas in *H. haydeni*, the *Rpm* is tilted backwards to form an erect plate with the adductor insertion surface on its posterior side (contrast Fig. 3A and B). As noted earlier, a similar contrast is seen also with respect to *H. lamberti*, as well as other, more derived polyconitid genera (Fig. 3 C, E, F).

On the other hand, co-eval species of *Polyconites* differ markedly from *Shajia* not only in their external form and ornamentation, as noted above, but also in the more extreme deflation of the *Rpm* (Fig. 3D). Furthermore, Sha and Cestari (2016) have drawn attention to the remarkable lack of records to date of *Polyconites* from the SW Asian Province (with the single exception of an unconfirmed mention of '*Polyconites* sp.', from Ladakh, by Mathur et al., 2008), weakening the circumstantial case for the derivation of *Shajia* from the latter genus.

Thus, by default, on the basis of the currently available evidence the most likely contender for the progenitor of *Shajia* is the species (or another, similar) represented by the specimen referred to *H. distefanoi* by Masse and Fenerci-Masse (2017; Fig.

19B therein), as discussed above. According to this scenario, *Shajia* would represent an iterative derivation of a *Polyconites*–like posterior myophoral organization from one of the 'third group' of *Horiopleura* species from the southern margin of the Mediterranean Tethys (extending to Oman) recognized by Masse and Fenerci-Masse (2017; pp. 75–76 therein). If correct, such a derivation would present an intriguing parallel with the appearance of another typically central to southern Tethyan form, *Sellaea* sp., in the Langshan fauna (Rao et al., 2015).

4.2. The composition and age of the rudist fauna of the Langshan Formation

Study of rudists from the Langshan Formation was first conducted by Yang et al. (1982). Six species assigned to four genera were described from Rutog County, including *Toucasia* sp., *Requienia*? sp., *Rutonia bangonghuensis* Yang et al., 1982 and three species of *Praeradiolites, P. hedini* Douvillé, 1916, *P. biconvexus* Yang et al., 1982 and *P. ngariensis* Yang et al., 1982. Gou (1994) and Gou and Shi (1998) described eight new species plus an undetermined ninth, assigned to three genera, from the Langshan Formation of Coqen, Bangoin and Gegyai counties, comprising seven species placed in *Praeradiolites, P. gegyainensis* Gou, 1994, *P. exiguous* Gou, 1994, *P. perbellus* Gou, 1994, *P. gregareus* Gou, 1994, *P. daxungensis* Gou and Shi, 1998, *P. bangoinensis* Gou and Shi, 1998, *P. coquenensis* Gou and Shi, 1998, together with *Coralliochama anomalusa* Gou and Shi, 1998, and *Gyropleura*? sp.

Scott et al. (2010) restudied the specimens described by Yang et al. (1982) and considered the rudist assemblage of the Langshan Formation to be Albian to Cenomanian in age. They suggested that *Monopleura* sp., had been mistaken for

385 *Toucasia* sp., by Yang et al. (1982); they assigned *Praeradiolites ngariensis* to
386 *Eoradiolites gilgitensis* based mainly on the structure of the anterior and posterior
387 radial bands; and they attributed *P. biconvexus* to the genus *Sphaerulites* based on the
388 external morphology.

389 Rao et al. (2015, 2017) revised the rudist taxa of the Langshan Formation
390 described by Yang et al. (1982), Gou (1994), and Gou and Shi (1998). A new genus,
391 *Auroradiolites,* was proposed for the endemic grouping of SW Asian to Japanese
392 radiolitid species characterised by a compact *ol*, which were formerly attributed to
393 *Praeradiolites* by Yang et al. (1982), Gou (1994), and Gou and Shi (1998).
394 *Eoradiolites* cf. *hedini*, *Magallanesia rutogensis* and *Sellaea* sp. were also recognized,
395 based on newly collected specimens. The age of the rudist assemblage reported by
396 Rao et al. (2015, 2017) is most likely late Aptian to Albian, as the age range of *A.*
397 *biconvexus* was revised to late Aptian to Albian by Rao et al. (2017).

398 As the age range of the Langshan Formation goes no younger than the early
399 Cenomanian, according to orbitolinid data (Boudagher-Fadel et al., 2017), the rudist
400 assemblage described from the Langshan Formation by Rao et al. (2015, 2017) is
401 most probably late Aptian–Albian in age, though a younger age cannot be excluded.

402 **4.3. Palaeobiogeographic implications**

403 *Horiopleura haydeni*, and *Auroradiolites gilgitensis,* which together constitute
404 the 'Yasin-type' rudist fauna (Skelton et al., 2005), were both first described by
405 Douvillé (1926) as new species from the Yasin Group of the Gilgit region, northern
406 Pakistan. This fossil site (Table1, No. 4) is located in the northern Kohistan terrane,

next to the North Suture Zone, which separates Kohistan from the Asian continent (Karakoram) to the north (Searle et al., 1999; Robertson and Collins, 2002; Khan et al., 2009). Subsequently, Pudsey et al. (1985) described rudists and orbitolinids from Kohistan, and proposed that the rudist-bearing limestone was of latest Aptian and/or early to middle Albian age.

[Table 1 hereabouts]

In the adjacent Ladakh terrane, *Horiopleura* sp., tentatively compared with *H. haydeni* by Upadhyay (2001), also co-occurs with *Auroradiolites gilgitensis*. This rudist assemblage was identified from limestones within the Saltoro Formation near the village of Shukur (Table1, No. 3) in the Nubra-Shyok valley region along the Shyok Suture Zone, which separates Ladakh from the Karakoram to the north (Upadhyay 2001, 2014). Upadhyay (2014) suggested a latest Aptian to early Albian age for this rudist assemblage.

Further west in Afghanistan, *Horiopleura haydeni* has been reported from two localities: Montenat et al. (1982) identified *H. haydeni* from the upper Aptian strata at the Adi Gar Mountains, about 30km north-northwest of Spin Boldak in the Kandahar region (Table1, No. 5); Rao et al. (2017) described two *H. haydeni* specimens, which were found together with *Auroradiolites gilgitensis*, from the Khist hills, south of Khash Rud, in central Afghanistan (Table1, No. 6).

Horiopleura haydeni thus has a relatively wide distribution extending along a nearly east-west-oriented belt in southwestern Asia, including central Afghanistan,

Kohistan in northern Pakistan and Ladakh in northern India (Fig. 7). These Yasin fauna species, *per se*, have not so far been recorded from the Lhasa Block, but instead *A. biconvexus* – probably derived from *A. gilgitensis* – and the canaliculate polyconitid genus *Magallanesia* were found there (Rao et al., 2015, 2017).

[Fig. 7 hereabouts]

Shajia tibetica was first recorded from Ladakh, as '*Polyconites* sp.', without detailed locality information, by Masse and Fenerci-Masse (2017). The specimens of *S. tibetica* recorded herein from the Langshan Formation of Nyima County, northern Lhasa Block (Fig. 7), were found in association with *A. biconvexus*, implying a late Aptian to Albian age (Rao et al., 2015), which is in broad agreement, moreover, with the generally accepted age of the Yasin fauna (Skelton et al., 2005; Sha and Cestari, 2016). Hence we conclude that *S. tibetica* and *A. biconvexus* can be regarded to be regional variants of the 'Yasin fauna'. Our material thus demonstrates that the Yasin fauna had already dispersed to the Lhasa Block by the late Aptian, which links the Langshan Formation palaeogeographically with other mid-Cretaceous sites of shallow-marine carbonate deposition in adjacent southwestern Asian regions.

The Kohistan–Ladakh terrane was situated between Asia to the north and India to the south in mid-Cretaceous times (Rolland et al., 2002). Although the exact timings of the collisions of the Kohistan–Ladakh terrane with Asia and with India, respectively, are still controversial (Rehman et al., 2011), it is generally accepted that the terrane itself was then located on the northern side of the Neo-Tethyan Ocean

(Chen et al., 1993; Searle et al., 1999). Meanwhile, according to the palaeogeographic reconstruction of Asia, central Afghanistan was situated on the southern Asian margin by mid-Cretaceous times (Chen et al., 1993; Zaman and Torii, 1999). At that time, the Lhasa Block had already collided with the Asian continent, and was also located at the northern margin of the Neo-Tethyan (Zhang, 2000; Leier et al., 2007). Therefore, all the localities that have yielded Yasin fauna were arrayed along or offshore from the southwestern Asian margin on the northern side of the Neo-Tethyan Ocean in the mid-Cretaceous.

As discussed above, in the SW Asian/Pacific Faunal Province, *Shajia* and *Horiopleura haydeni* were restricted to the southwestern Asia region. The genus *Praecaprotina* of late Aptian–Albian age has only been recorded from Japan and the Daiichi–Kashima Guyot in the Northwest Pacific (Masse and Shiba, 2010). The canaliculate polyconitid genus *Magallanesia*, of likely late Albian age, was found not only on Cebu Island and Takuyo–Daini Seamount, both located in the Pacific region (Sano et al., 2014), but also on the Lhasa Block in southwestern Asia (Rao et al., 2015). These polyconitid taxa, are all endemic to the combined southwestern Asia and Pacific regions, and mostly co-occur with the radiolitid genus *Auroradiolites*, which is characterised by an entirely compact outer shell layer and is also restricted to these regions (Rao et al., 2017). Hence these findings suggest strong endemism in the rudist fauna of the SW Asian/Pacific Faunal Province during the late Aptian to Albian interval.

5. Conclusions

Shajia tibetica gen. et sp. nov., a new polyconitid rudist, is described from the Langshan Formation of Nyima County in the northern Lhasa Block of Tibet. It is similar in external form to *Horiopleura haydeni* Douvillé, 1926, an abundant species of late Aptian to Albian age that is endemic to southwestern Asia, including Afghanistan, Kohistan in northern Pakistan, and Ladakh in northern India. However, *Shajia* differs from the latter species in its posterior myophoral arrangement: 1) *Lpm* is strongly bent posteriorly, such that it is nearly parallel to the over-arching posterior shell wall of the *LV*, thereby forming a sub-rectangular ectomyophoral cavity between them; 2) *Rpm* is formed by an inward-inclined swelling of the inner shell layer, without forming a projecting plate. A single specimen from Ladakh which was assigned to *Polyconites*? sp. by Masse and Fenerci-Masse (2017), is reappraised and transferred to *Shajia*. It was most likely derived from one of a small group of *Horiopleura* species that dwelt on the southern margin of the Mediterranean Tethys (extending to Oman) and which show a posterior myophoral arrangement approaching that of *Shajia*. The geological range of *Shajia* is probably Upper Aptian to Albian, combining the records from the Lhasa Block and Ladakh.

S. tibetica is associated with *A. biconvexus*, and as the age of the association is basically in accordance with that of the Yasin fauna (*H. haydeni* and *A. gilgitensis*) it may thus be considered as a regional variant of the latter association. This new material thus shows that the Yasin fauna had already dispersed to the Lhasa Block by the late Aptian, making the Langshan Formation comparable palaeobiogeographically with other mid-Cretaceous shallow-water carbonate deposits in adjacent southwestern

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505 **References**

506 BOUCHET, P., ROCROI, J.-–P., BIELER, R., CARTER, J.G. and COAN, E.V., 2010.
507 Nomenclator of Bivalve Families (P. B. and J.-–P. R.) and Classification of Bivalve
508 Families (R.B., J.G.C. and E.V.C.). *Malacologia*, **52**, 1−184.

509 BOUDAGHER-–FADEL, M. K., HU, X., PRICE, G. D., SUN, G., WANG, J. and AN,
510 W., 2017. Foraminiferal Biostratigraphy and Palaeoenvironmental Analysis of the
511 Mid--Cretaceous Limestones in the Southern Tibetan Plateau. *Journal of*
512 *Foraminiferal Research*., **47(2)**, 188−207. (in press).

513 CHEN, Y., COURTILLOT, V., COGNÉ, J. P., BESSE, J., YANG, Z. and ENKIN, R.,

514 1993. The Configuration of Asia Prior to the Collision of India: Cretaceous
515 Paleomagnetic Constrains. *Journal of Geophysical Research*, **98**, 927−941.
516 CHERCHI, A. and SCHROEDER, R., 2013. The *Praeorbitolina*/*Palorbitolinoides*
517 Association: an Aptian Biostratigraphic Key-–Interval at the Southern Margin of
518 the Neo-–Tethys. *Cretaceous Research*, **39**, 70−77.
519 CUVILLIER, J. AND SZAKALL, V., 1949. Foraminifères d'Aquitaine, Première
520 partie (Reophacidae à Nonionidae), Boisseau Imp., Toulouse, 112 pp.
521 D'ORBIGNY, A. D., 1847. Sur les Brachiopodes ou Palliobranches (deuxième
522 Mémoire). *Comptes Rendus Hebdomadaires des Séances de l'Académie des*
523 *Sciences (Paris)*, **25**, 266–269.
524 DECELLES, P. G., KAPP, P., DING, L. and GEHRELS, G. E., 2007. Late
525 Cretaceous to middle Tertiary basin evolution in the central Tibetan Plateau:
526 Changing environments in response to tectonic partitioning, aridification, and
527 regional elevation gain. *Geological Society of America Bulletin*, **119 (5-–6)**, 654–
528 680.
529 DENG, Z. Q. and WANG, G. X., 2013. Mesozoic Corals and Sponges from Gê'gyai
530 and Rutog, Xizang. *Acta Palaeontoligica Sinica*, **52**, 202−212. [In Chinese with
531 English abstract]
532 DI STEFANO, G., 1889. Studi stratigrafici e paleontologici sul sistema Cretaceo della
533 Sicilia. 1. Gli strati con *Caprotina* di Termini-–Imerese. *Atti della Reale Accademia*
534 *di Scienze, Lettere e Belle Arte di Palermo*, Nuova Serie, **10**, 1–44.
535 DOUVILLÉ, H., 1889. Sur quelques rudistes du terrain crétacé inférieur des Pyrénées.

Bulletin de la Société géologique de France, (3), **17**, 627–635.

DOUVILLÉ, H., 1909. Sur le genre *Eoradiolites* nov. *Comptes Rendus des Séances de la Société Géologique de France* (série 4), **9**, 77.

DOUVILLÉ, H., 1916. Les calcaires a Orbitolines et a Radiolites du Thibet. 145–147. In HEDIN, S. (ed.) *Southern Tibet – Discoveries in former times compared with my own researches in 1906–1908. Vol. 5 Petrographie und Geologie I*. Beschreibung der Gesteinsproben, Anhang. Lithographic Institute of the General Staff of the Swedish Army, Stockholm.

DOUVILLÉ, H., 1926. Fossiles recueillis par Hayden dans le Kashmir en 1906 et les Pamirs en 1914; leur description. *Records of the Geological Survey of India*, **58**, 349–357.

ERMAN, A., 1854. Einige Beobachtungen über die Kreideformation an der Nordküste von Spanien. Zeitschrift der Deutschen. *Geologischen Gesellschaft*, **6**, 596–611.

GOU, Z. H. and SHI, H., 1998. Rudists (Bivalvia) from the Cretaceous of Tibet, China, with Descriptions of New Species. 255–266. *In* JOHNSON, P.A. and HAGGART, J.W. (eds.). *Bivalves: an eon of evolution – paleobiological studies honoring Norman D. Newell*. University of Calgary Press, Calgary, Canada, 461 pp.

GOU, Z. H., 1994. Rudists Fossils of Cretaceous Period in Gegyai Region, Tibet. *Tibet Geology*, **12**, 128–138. [In Chinese with English abstract]

HAY, W.W., DeCONTO, R., WOLD, C.N., WILSON, K.M., VOIGHT, S., SCHULZ,

M., WOLD-–ROSSBY, A., DULLO, W.-–C., RONOV, A.B., BALUKHOVSKY, A.N. and SOEDING E., 1999. Alternative Global Cretaceous Palaeogeography. *In* BARRERA, E. and JOHNSON, C. (eds.). *The Evolution of Cretaceous Ocean/Climate Systems, Geological Society of America Special Paper*, **332**, 1–47.

HENSON, F .R. S., 1948. Larger imperforate foraminifera of south-western Asia. Families Lituolidae, Orbitolinidae and Meandropsinidae. *Monograph British Museum* (*Natural History*), London, 127pp.

KAPP, P., DECELLES, P. G., GEHRELS, G. E., HEIZLER, M. AND DING, L., 2007. Geological records of the Lhasa-–Qiangtang and Indo-–Asian collisions in the Nima area of central Tibet. *Geological Society of America Bulletin*, **119 (7-–8)**, 917–933.

KHAN, S. D., WALKER, D. J., HALL, S. A., BURKE, K. C., SHAH, M. T. and STOCKLI, L., 2009. Did the Kohistan-–Ladakh Island Arc Collide First with India? *Geological Society of America Bulletin*, **121**, 366–384.

LEEDER, M. R., SMITH, A. B., and JIXIANG, Y., 1988. Sedimentology, Palaeoecology and Palaeoenvironmental Evolution of the 1985 Lhasa to Golmud Geotraverse. *Royal Society of London, Philosophical Transactions, Series A*, **327**, 107–143.

LEIER, A. L., DECELLES, P. G., KAPP, P. and GEHRELS, G. E., 2007. Lower Cretaceous Strata in the Lhasa Terrane, Tibet, with Implications for Understanding the Early Tectonic History of the Tibetan Plateau. *Journal of Sedimentary Research*, **77**, 809–825.

LEYMERIE, A., 1878, 1881. Description Géologique et Paléontologique des Pyrénées de la Haute-Garonne. E. Privat, Toulouse, 2 v. [text (1878): 1010 p. atlas (1881)].

LI, Z., DING, L., SONG, P., FU, J. and YUE, Y., 2017. Paleomagnetic Constraints on the Paleolatitude of the Lhasa Block during the Early Cretaceous: Implications for the Onset of India – Asia Collision and Latitudinal Shortening Estimates Across Tibet and Stable Asia. *Gondwana Research*, **41**, 352–372.

LÖSER, H. and LIAO, W. H., 2001. Cretaceous Corals from Tibet (China) -– Stratigraphic and Palaeobiogeographic Aspects. *Journal of Asian Earth Sciences*, **19**, 661−667.

MAC GILLAVRY, H. J., 1937. Geology of the Province of Camagüey, Cuba, with Revisional Studies in Rudist Paleontology. *Geographische en Geologische Mededeelingen, Physiographisch-–Geologische Reeks*, **14**, 168 pp.

MASSE, J. P. and FENERCI--MASSE, M., 2017. Taxonomy and Stratigraphy of Late Barremian–Albian Species of *Horiopleura* Douvillé (Hippuritida, Polyconitidae) of the Mediterranean and Southwestern Asian Regions. *Cretaceous Research*, **76**, 53–80.

MASSE, J. P., ARIAS, C. and VILAS, L., 1998. Lower Cretaceous Rudist Faunas of Southeast Spain: an Overview. *In*: MASSE, J. P., SKELTON, P.W. (Eds.), *Quatrième Congrès International sur les Rudistes*, Géobios, Mémoire Spécial, **22**, 193−210.

MASSE, J. P., MOURGES, F. A. and FENERCI-MASSE. M., 2015. Aptian–Albian

Rudist Bivalves (Hippuritida) from the Chilean Central Andes: Their Palaeoceanographic Significance. *Cretaceous Research*, **54**, 243–254.

MASSE, J.P. and SHIBA, M., 2010. *Praecaprotina kashimae* nov. sp. (Bivalvia, Hippuritacea) from the Daiichi-–Kashima Seamount (Japan Trench). *Cretaceous Research*, **31(2)**, 147–153.

MATHUR, N.S., JUYAL, K.P. and KUMAR, K. 2008. Biotic response to Cretaceous-–Eocene tectonic events at the northern margin of the Indian Plate and the Indus-–Tsangpo Suture Zone, Ladakh Himalaya, India. *Journal of the Palaeontological Society of India*, **53**, 37-–49.

METCALFE, I., 2006. Palaeozoic and Mesozoic Tectonic Evolution and Palaeogeography of East Asian Crustal Fragments: The Korean Peninsula in Context. *Gondwana Research*, **9**, 24–46.

MONTENAT, C., MOULLADE, M. and PHILIP, J., 1982. Le Crétacé inférieur à Orbitolines et Rudistes d'Afghanistan central. *Géologie Méditerranéenne*, **9**, 109–122.

NEWELL, N. D., 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 1–25.

PAN, G., WANG, L., LI, R., YUAN, S., JI, W., YIN, F., ZHANG, W. and WANG, B., 2012. Tectonic Evolution of the Qinghai-–Tibet Plateau. *Journal of Asian Earth Sciences*, **53**, 3–14.

PARONA, C.F., 1909. La fauna coralligena del Cretaceo dei Monti d'Ocre nell'Abruzzo aquilano. *Memoria per servire alla descrizione della carta geologica*

624 *d'Italia*, **5**, 1-–233.

625 PUDSEY, C. J., SCHROEDER, R. and SKELTON, P. W., 1985. Cretaceous
626 (Aptian/Albian) Age for Island-–Arc Volcanics, Kohistan, N. Pakistan. 150–168. *In*
627 GUPTA, V. J. (ed.). *Contributions to Himalayan Geology, v. 3, Geology of western*
628 *Himalayas*. Hindustan Publishing Corporation, Delhi.

629 RAO, X., SKELTON P. W., SANO S., LI, C., PAN, Y., LUO, H., CAI, H., PENG, B.
630 and SHA, J., 2017. Evolution and Palaeogeographical Dispersion of the Radiolitid
631 Rudist genus *Auroradiolites* (Bivalvia: Hippuritida), with Descriptions of New
632 Material from Tibet and Archived Specimens from Afghanistan, *Papers in*
633 *Palaeontology*, **3(2)**, DOI: 10.1002/spp2.1076.

634 RAO, X., SKELTON, P.W., SHA, J., CAI, H. and IBA, Y., 2015. Mid--Cretaceous
635 Rudists (Bivalvia: Hippuritida) from the Langshan Formation, Lhasa block, Tibet.
636 *Papers in Palaeontology*, **1**, 401–424.

637 REHMAN, H. U., SENO, T., YAMAMOTO, H. and KHAN, T., 2011. Timing of
638 Collision of the Kohistan-–Ladakh Arc with India and Asia: Debate. *Island Arc*, **20**,
639 308–328.

640 ROBERTSON, A. H. F. and COLLINS, A. S., 2002. Shyok Suture Zone, N Pakistan:
641 Late Mesozoic–Tertiary Evolution of a Critical Suture Separating the Oceanic
642 Ladakh Arc from the Asian Continental Margin. *Journal of Asian Earth Science*, **20**,
643 309–351.

644 ROEMER, F., 1849. *Texas*. Bonn, 464 pp.

645 ROLLAND, Y., PICARD, C., PÊCHER, A., LAPIERRE, H., BOSCH, D. and

KELLER, F., 2002. The Ladakh Arc of NW Himalaya: Slab Melting and Mantle Interaction During Fast Northward Drift of Indian Plate. *Chemical Geology*, **182**, 139–178.

ROSSI RONCHETTI, C., 1965. Rudiste e nerinee del cretaceo di Yasin (Pakistan nord-–occidentale). *In* DESIO A. (leader), BRILL E. J. (eds) *Italian Expeditions to the Karakorum (K2) and Hindu Kush, Scientific Reports*. Part 4, 229-–272. Leiden.

ROULLAND, F., 1830. Nouvelles observations sur les *Ichthyosarcolites*. Actes de la Société Linéenne de Bordeaux, **4**, 164–166.

SAHNI, M. R., 1937. Discovery of *Orbitolina*-bearing Rocks in Burma, with a Description of *Orbitolina birmanica* sp. nov. *Records of the Geological Survey of India*, **71 (4)**, 360–375.

SANO, S. and MASSE, J. P., 2013. First record of a primitive radiolitid rudist from Japan. *Paleontological Research*, **17**, 317–324.

SANO, S., IBA, Y., SKELTON, P. W., MASSE, J.-–P. AGUILAR, Y. M. and KASE, T., 2014. The Evolution of Canaliculate Rudists in the Light of a New Canaliculate Polyconitid Rudist from the Albian of the Central Pacific. *Palaeontology*, **57**, 951–962.

SCARLATO, O. A. and STAROBOGATOV, Y. I., 1971. Osnovnye Cherty Evolyutsii i sistema Klassa Bivalvia Morfologiya, Sistematika i Filogeniya Mollyuskov. *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR*, **80**, 5–38. [In Russian]

SCHLAGINTWEIT, F. and WILMSEN, M., 2014. Orbitolinid Biostratigraphy of the Top Taft Formation (Lower Cretaceous of the Yazd Block, Central Iran).

Cretaceous Research, **49**, 125–133.

SCHROEDER, R. and CONRAD, M. A., 1968. Huitième note sur les Foraminifères du Crétacé inférieur de la région genevoise. *Eopalorbitolina charollaisi*, n. gen., n. sp., un Orbitolinidé nouveau du Barrémien à faciès urgonien. Compte rendu des séances de la Société de Physique et d'Histoire Naturelle de Genève, nouvelle série, **2(3)**, 145–162.

SCOTT, R. W., WAN, X., SHA, J. and WEN, S., 2010. Rudists of Tibet and Tarim Basin, China: Significance to Requieniidae Phylogeny. *Journal of Paleontology*, **84**, 444–465.

SEARLE, M. P., KHAN, M. A., FRASER, J. E., GOUGH, S. J. and JAN, M. Q., 1999. The Tectonic Evolution of the Kohistan Collision Belt Along the Karakoram Highway Transect, North Pakistan. *Tectonics*, **18**, 929–949.

SHA, J. and CESTARI, R., 2016. Late Aptian-–Albian Yasin--type Rudist Assemblage in the Himalayas: Palaeobiogeographic Implications. *Cretaceous Research*, **65**, 34–47.

SKELTON, P. W. and MASSE, J.-–P., 1998. Revision of the Lower Cretaceous Rudist Genera *Pachytraga* Paquier and *Retha* Cox (Bivalvia: Hippuritacea), and the origins of the Caprinidae. *Géobios, mémoire spécial*, **22**, 331–370.

SKELTON, P. W., 2013a. Rudist Classification for the Revised Bivalvia Volumes of the 'Treatise on Invertebrate Paleontology'. *Caribbean Journal of Earth Science*, **45**, 9–33.

SKELTON, P. W., 2013b. Rudist Classification: Nomenclatural Correction of

690 'Suborder Radiolitidina Skelton, 2013' to 'Suborder Hippuritidina Newell, 1965'.
691 *Caribbean Journal of Earth Science*, **45**, 34.
692 SKELTON, P. W., 2018. Part N, Volume 1, Chapter 26A: Introduction to the
693 Hippuritida (rudists): Shell structure, anatomy, and evolution. *Treatise Online*
694 104:1–37.
695 SKELTON, P. W., SANO, S. and MASSE, J.-–P., 2013. Rudist Bivalves and the
696 Pacific in the Late Jurassic and Early Cretaceous. *Journal of the Geological Society*,
697 **170**, 513–526.
698 SKELTON, P.W. and MASSE, J. P., 2000. Synoptic Guide to the Lower Cretaceous
699 Rudist Bivalves of Arabia. *SEPM Special Publication*, **69**, 85–95.
700 SKELTON, P.W. and SMITH, A.D., 2000. A Preliminary Phylogeny for Rudist
701 Bivalves: Sifting Clades from Grades. *In*: HARPER, E.M., TAYLOR, J.D.,
702 CRAME, J.A. (Eds.), *the Evolutionary Biology of the Bivalves*. Geological Society,
703 London. Special Publication, **177**, 97–127.
704 SKELTON, P.W., GILI, E., BOVER-–ARNAL, T., SALAS, R. and MORENO-–
705 BEDMAR, J.A., 2010. A New Species of *Polyconites* from the Lower Aptian of
706 Iberia and the Early Evolution of Polyconitid Rudists. *Turkish Journal of Earth*
707 *Sciences*, **19**, 557–572.
708 SKELTON, P.W., RAISOSSADAT, N., UPADHYAY, R. and BERNOULLI, D.
709 2005. 'Yasin--type' rudist fauna from eastern Iran and northern Ladakh. In
710 FILKORN, H.N. (Ed.), SEPM Abstracts and Post-–congress Field Guide, Seventh
711 International Congress on Rudists, p. 91. Austin. ISBN 1565761197.

SMOUT, A. H., 1956. Three new Cretaceous genera of foraminifera related to the Ceratobuliminidae. *Micropaleontology*, **2**, 335–348.

STEUBER, T., 1999. Cretaceous Rudists of Boeotia, Central Greece. *Special Papers in Palaeontology,* **61**, 229 pp.

UPADHYAY, R., 2001. Middle Cretaceous Carbonate Build-–Ups and Volcanic Seamount in the Shyok Suture, Northern Ladakh, India. *Current Science*, **81**, 695–699.

UPADHYAY, R., 2014. Palaeogeographic Significance of 'Yasin--type' Rudist and Orbitolinid Fauna of the Shyok Suture Zone, Saltoro Hills, Northern Ladakh, India. *Current Science*, **106**, 223–228.

WANG, L., PAN, G., DING, J., and YAO, D., 2013. *Geological Mapping illumination (1:1500000) of Qinghai–Tibet Plateau and Its adjacent area*. Geological Publishing House, Beijing. 288pp. [In Chinese]

XZBGM (XIZANG BUREAU OF GEOLOGY and MINERAL RESOURCES), 1993. *Regional geology of Xizang Autonomous Region*. Geological Publishing House, Beijing. 707pp. [In Chinese with English summary]

YABE, H. and NAGAO, S., 1926. *Praecaprotina*, nov. gen. from the Lower Cretaceous of Japan. *Science Reports of the Tohoku Imperial University, Second Series*, **9**, 21–24.

YANG, T., MA, Y., ZHANG, S., BIAN, W., YANG, Z., WU, H., LI, H., CHEN, W. and DING, J., 2015. New Insights into the India ‐ Asia Collision Process from Cretaceou Paleomagnetic and Geochronologic Results in the Lhasa Terrane.

Gondwana Research, **28**, 625–641.

YANG, Z., NIE, Z., WU, S. and LIANG, D., 1982. Cretaceous Rudists from Ngari, Xizang (Tibet), Autonomous Region, China and Their Geologic Significance. *Acta Geologica Sinica*, **56**, 293–301. [In Chinese with English abstract]

YEHARA, S., 1920. A Pachyodont Lamellibranchia from the Cretaceous Deposits of Miyako in Rikuchu. *Journal of the Geological Society of Tokyo*, **27**, 39–44.

YIN, A. and HARRISON, T. M., 2000. Geologic Evolution of the Himalayan-–Tibetan Orogen. *Annual Review of Earth and Planetary Sci*ences, **28**, 2211–2280.

YU, W. and XIA, J. B., 1985. Late Jurassic−Cretaceous Nerineids from Northern Xizang. *Acta Palaeontoligica Sinica*, **24**, 640−650. [In Chinese with English abstract].

ZAMAN, H. and TORII, M., 1999. Paleomagnetic Study of Cretaceous Red Beds from the Eastern Hindukush Ranges, Northern Pakistan; Paleoarc Construction of the Kohistan-–Karakoram Composite Unit before the India-–Asia Collision. *Geophysical Journal International*, **136**, 719–738.

ZHANG, B. G., 1982. *Orbitolina* (Foraminifera) from Xizang. 51−80. *In The Series of the Scientific Expedition to the Qinghai-–Xizang (Tibet) Plateau, Paleontology of Xizang (Tibet), 4*. Science Press, Beijing. [In Chinese with English abstract].

ZHANG, B. G., 1986. Early Cretaceous Orbitolinids from Xainza and Baingoin, Xizang. *In Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **10**, 101−122. [In Chinese with English abstract].

ZHANG, B. G., 1991. Cretaceous Larger Foraminifera Orbitolines from Ngari,

Western Xizang (Tibet). 68−87. *In* SUN, D. L., XU, J. T. et al. (eds). *Stratigraphy and Palaeontology of Permian, Jurassic and Cretaceous from the Rutog Region, Xizang (Tibet)*. Nanjing University Press, Nanjing. [In Chinese with English abstract].

ZHANG, B. G., YANG, S. Q., SUN, D. L. and YE, C. H., 1986. Cretaceous System. *In Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **10**, 46−55. [In Chinese with English abstract].

ZHANG, K. J., 2000. Cretaceous Palaeogeography of Tibet and Adjacent Areas (China): Tectonic Implications. *Cretaceous Research*, **21**, 23−33.

ZHANG, K. J., XIA, B. D., WANG, G. M., LI, Y. T. and YE, H. F., 2004. Early Cretaceous Stratigraphy, Depositional Environments, Sandstone Provenance, and Tectonic Setting of Central Tibet, Western China. *Geological Society of America, Bulletin*, **116**, 1202–1222.

ZHU, D., ZHAO, Z., NIU, Y., DILEK, Y., HOU, Z. and MO, X., 2013. The Origin and Pre-–Cenozoic Evolution of the Tibetan Plateau. *Gondwana Research*, **23**, 1429–1459.

774 **Table caption**

775 Table 1. Localities yielding *Shajia* and *Horiopleura haydeni* in the SW Asian/Pacific
776 Faunal Province, with currently assigned ages. See Fig. 7 for the geographical
777 distribution of these localities.

778

779 **Figure Captions**

780 1. Location of study area. (A) Map showing the tectonic framework of Tibet and the
781 outcrops of the Langshan Formation (grey) in the Lhasa Block (after XZBGM,
782 1993; Wang et al., 2013). (B) Locality map for *Shajia* in Nyima County (red
783 rectangle in A). *Abbreviations*: BNS, Bangong–Nu Suture; IYS, Indus–Yarlung
784 Suture.

785 [in colour]

786 2. Abbreviations of quantitative characters used for the description of *Shajia* (*LV*,
787 left valve; *RV*, right valve): *Dap*, antero-posterior commissural diameter, *Ddv*,
788 dorso–ventral commissural diameter; *Hd*, dorsal height of *RV*; *Hv*, ventral height
789 of *RV*; *LVc*, convexity of the *LV*.

790 [in black and white]

791 3. Diagrammatic antero-posterior sections across both valves of *Shajia* and other
792 similar polyconitids (outer shell layer shown in black; inner shell, in grey). A,
793 *Shajia* (based on Fig. 5D herein); B, *Horiopleura haydeni* (after Rossi Ronchetti,
794 1965, Plate 38, fig. 1; outer shell layer worn, and image reversed to facilitate
795 comparison); C, *Horiopleura lamberti* (after Skelton and Smith, 2000, Fig. 7); D,
796 *Polyconites* (after Skelton, 2013a, Fig. 7A); E, *Praecaprotina yaegashii* (after

797 Sano et al., 2014, Fig. 2); F, *Magallanesia canaliculata* (after Sano et al., 2014,
798 Fig. 4D). Abbreviations: *Lam*, anterior myophore of left valve; *Lpm*, posterior
799 myophore of left valve; *LV*, left valve; *Ram*, anterior myophore of right valve;
800 *Rpm*, posterior myophore of right valve; *RV*, right valve.
801 [in black and white]
802 4. *Shajia tibetica* gen. et sp. nov., holotype articulated specimen (NIGP. 110522). A,
803 dorsal view showing overhanging umbo of *LV*. B, ventral view. C, anterior view
804 showing the oblique commissure and the convexity of the *LV*; red lines show the
805 two sections made on this specimen; a, b, c, and d represent the positions of the
806 sections shown in Figs. 5A–D respectively. D, posterior view of *RV* showing the
807 longitudinal ribs (inset: magnified view of red rectangle).
808 [in colour]
809 5. *Shajia tibetica* gen. et sp. nov., holotype (NIGP. 110522): A–D, successively
810 more ventrally situated antero-posterior sections of both valves, as indicated either
811 side of the red lines in Fig. 4C (B and D are reversed so that all images are viewed
812 looking dorsally, for ease of comparison): A–B show the dentition; C–D show the
813 myophoral organisation. Abbreviations: *at*, anterior tooth (from *LV*); *ct*, central
814 tooth (from *RV*); *Lam*, anterior myophore of left valve; *Lpm*, posterior myophore
815 of left valve; *LV*, left valve; *o*, annexe extending dorsally from the ectomyophoral
816 cavity; *pt*, posterior tooth (from *LV*); *Ram*, anterior myophore of right valve; *Rpm*,
817 posterior myophore of right valve; *RV*, right valve.
818 [in colour]

6. *Shajia tibetica* gen. et sp. nov., paratype articulated specimen (NIGP. 110523). A, dorsal view, commissure indicated by dashed red line; solid red lines show the three transverse sections made of this specimen. B, anterior view showing the longitudinal ribs on the *RV*. C, D–E and F show the three successively lower transverse sections indicated in A, all in adumbonal view of the *RV*, revealing the myocardinal organisation.

   Abbreviations: *at*, anterior tooth (from *LV*); *ct*, central tooth (from *RV*); *Lig*, infolding of outer shell layer associated with invaginated ligament; *Lpm*, posterior myophore of left valve (dorsalmost part only); *LV*, left valve; *o*, annexe extending dorsally from the ectomyophoral cavity; *ol*, outer shell layer (of *RV*); *pt*, posterior tooth (from *LV*); *Ram*, anterior myophore of right valve; *Rpm*, posterior myophore of right valve; *RV*, right valve.

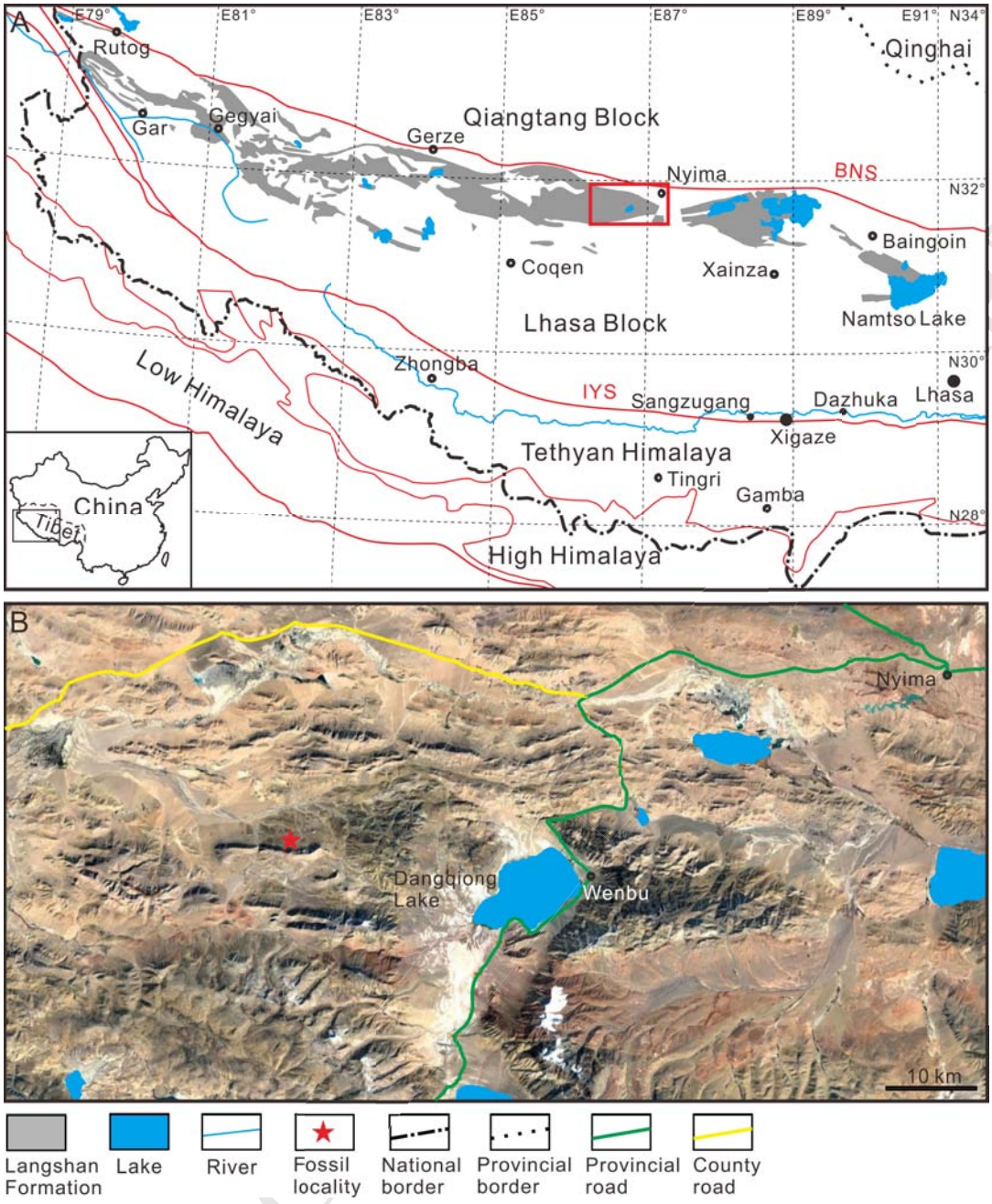
[in colour]

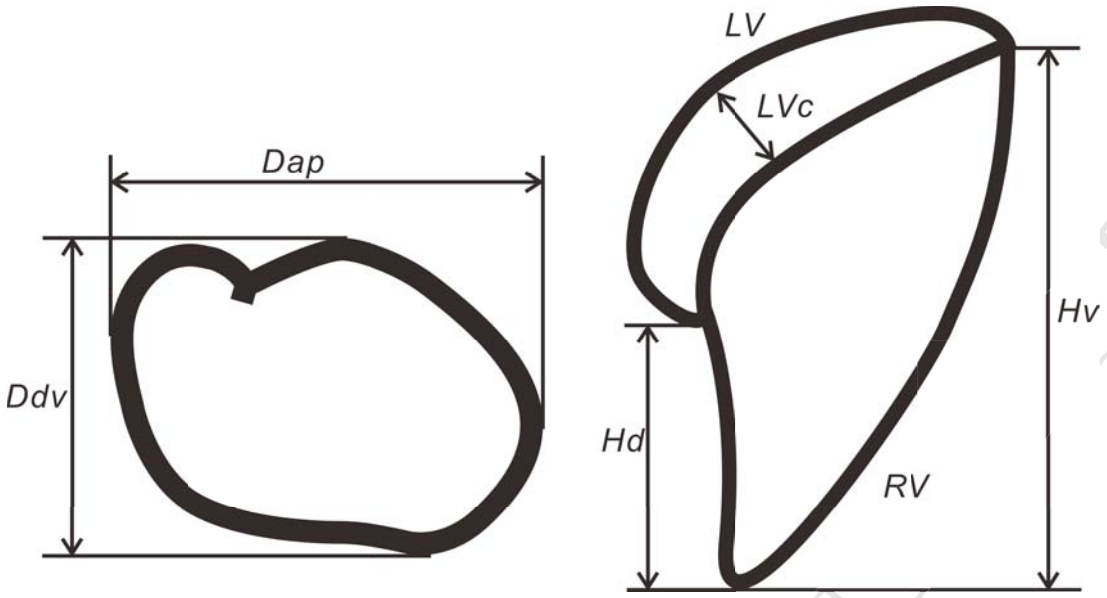
7. Present-day geographical map showing the fossil localities bearing *Shajia* and *Horiopleura haydeni*, represented by red and blue stars respectively (see Table 1 for details). The base map was generated using the ODSN online Plate Tectonic Reconstruction Service (Hay et al., 1999). CAF, central Afghanistan; KOH–LAD, Kohistan–Ladakh terrane; LSA, Lhasa block.

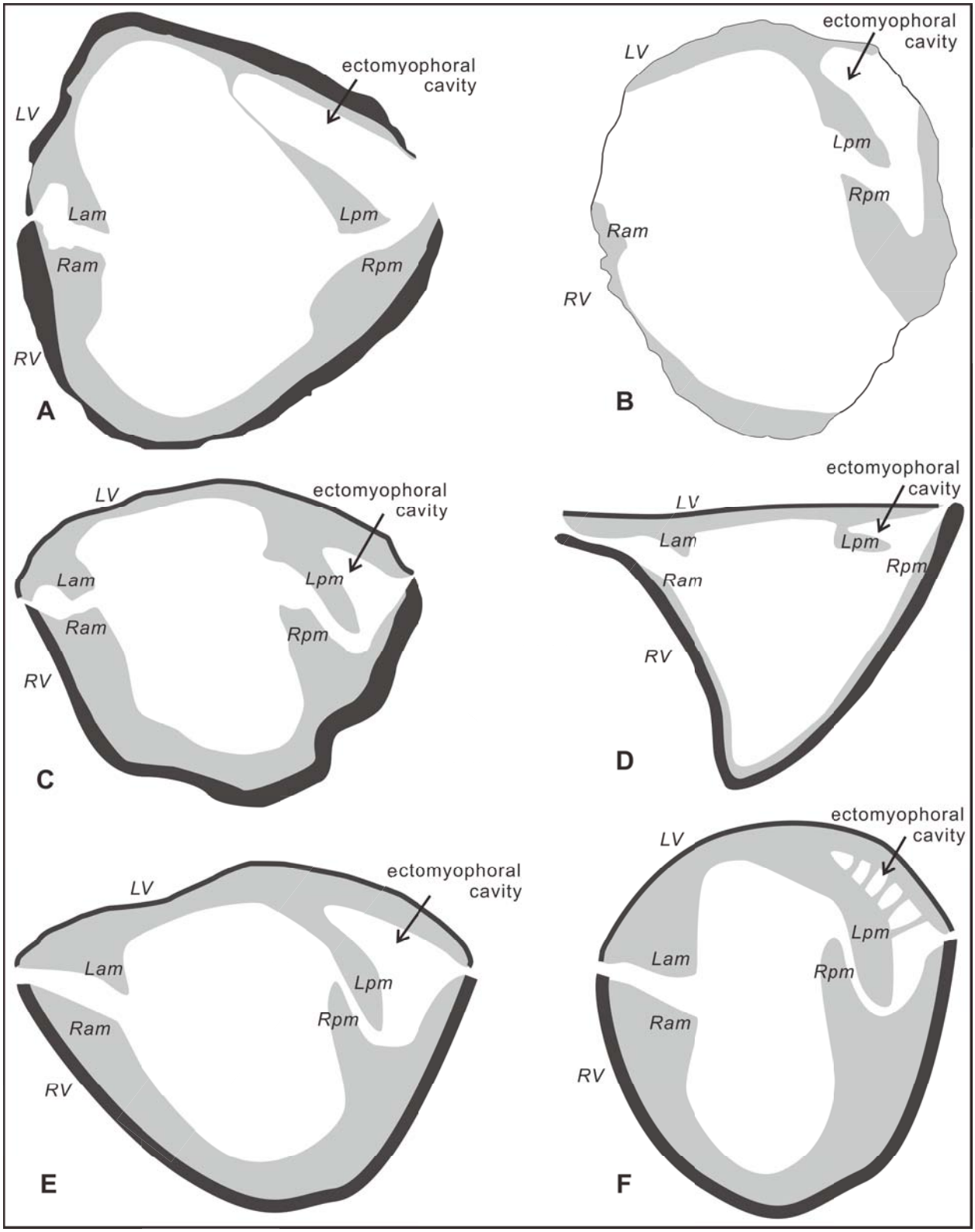
[in colour]

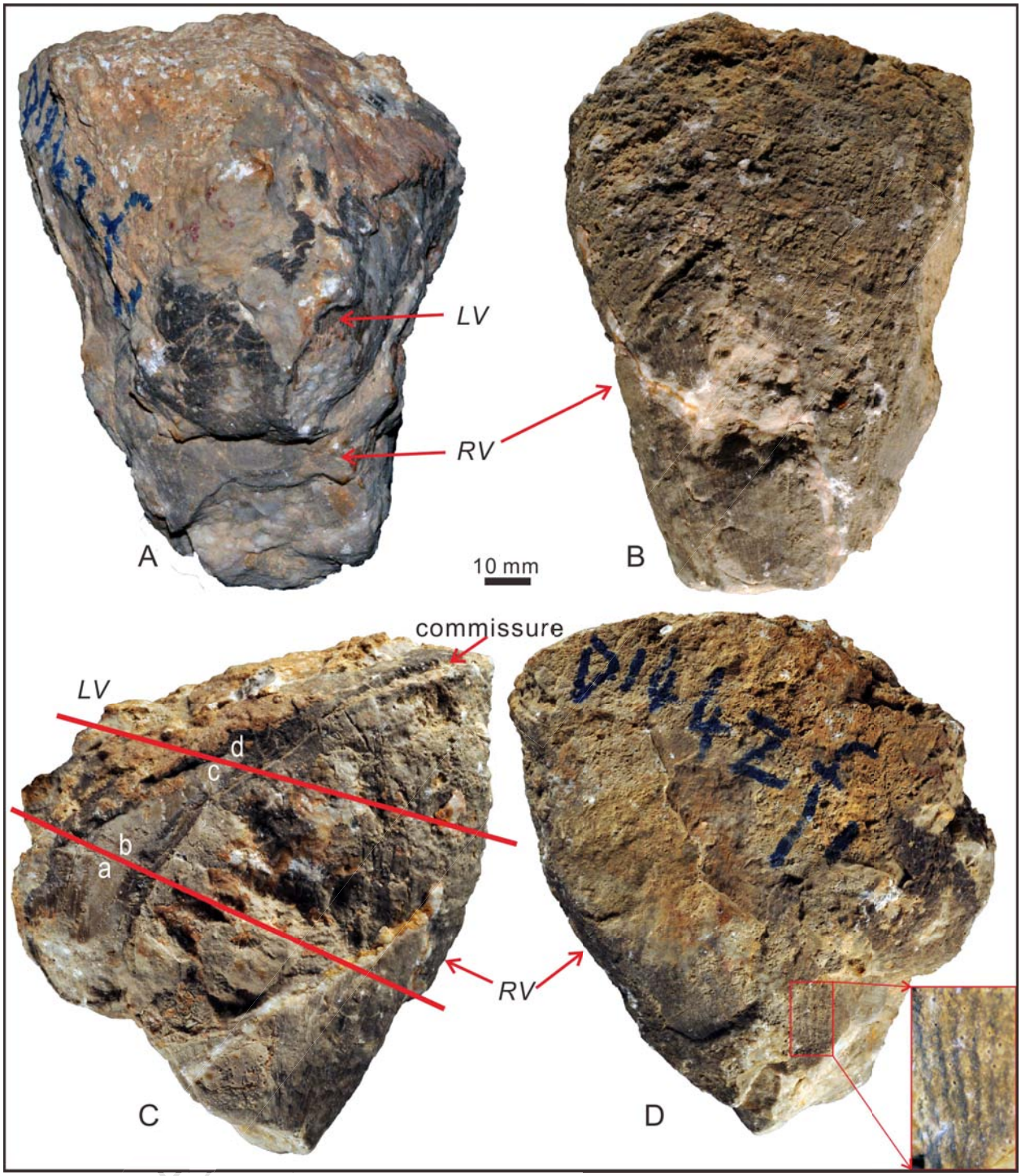
Table 1

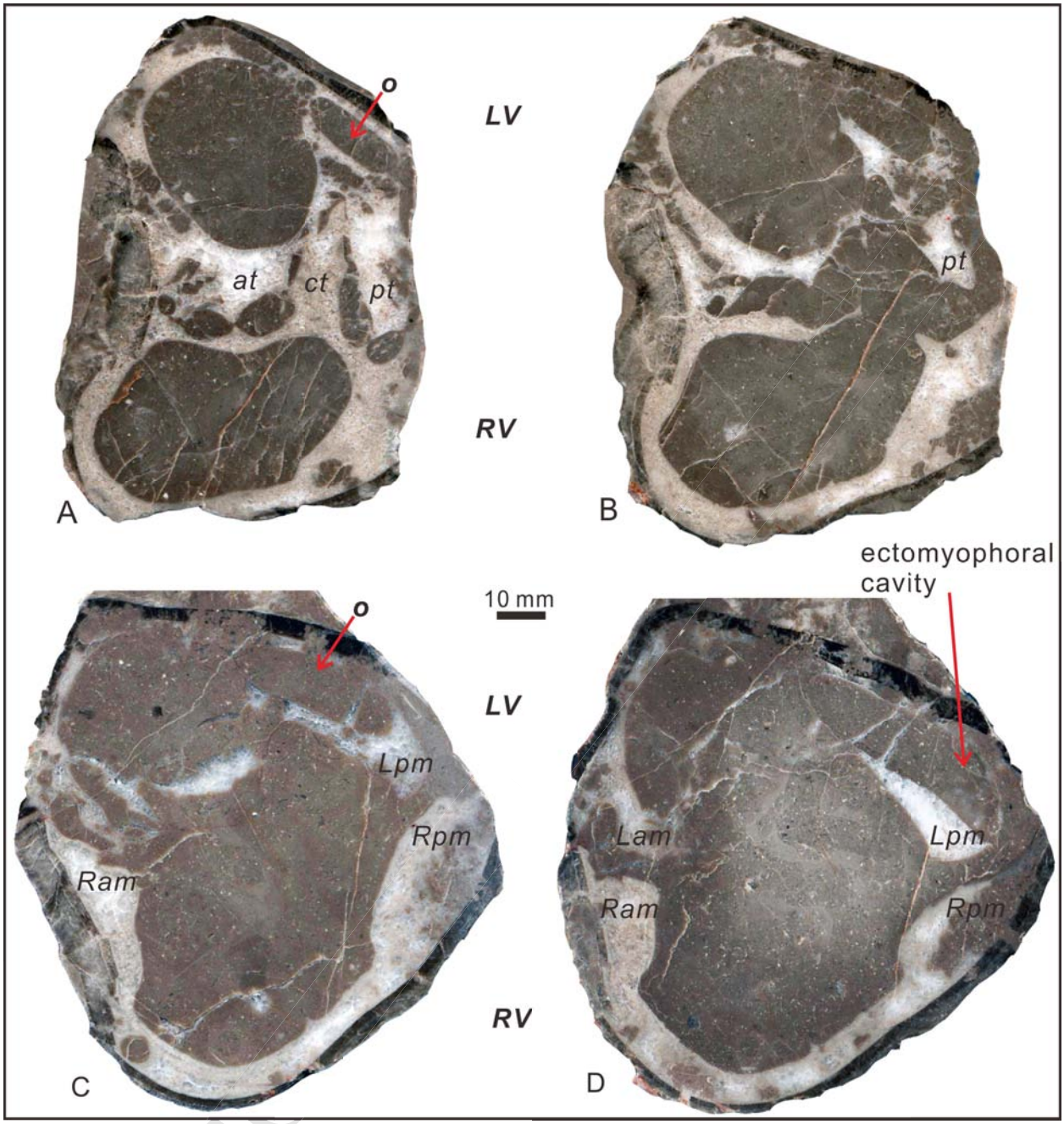
Record	Locality	Age	Species	References
1	Nyima County, Tibet, Southeast China	late Aptian to Albian	*Shajia tibetica*	This paper
2	Ladakh, North India	late Aptian	*S. tibetica* (='*Polyconites* sp.')	Masse and Fenerci-Masse, 2017
3	Shukur, Nubra-Shyok valley, Ladakh, North India	latest Aptian to early Albian	*Horiopleura haydeni*	Upadhyay, 2001, 2014
4	Yasin, Gilgit region, Kohistan, Northwest Pakistan	latest Aptian to middle Albian	*H. haydeni*	Douvillé, 1926; Rossi Ronchetti, 1965; Pudsey et al., 1985; Sha and Cestari, 2016
5	Adi Gar Mt. (about 30 km N.N.W. from Spin Boldak) in Kandahar, Central Afghanistan	late Aptian	*H. haydeni*	Montenat et al., 1982
6	Khist hills, south of Khash Rud, Central Afghanistan	latest Aptian to middle Albian	*H. haydeni*	Rao et al., 2017

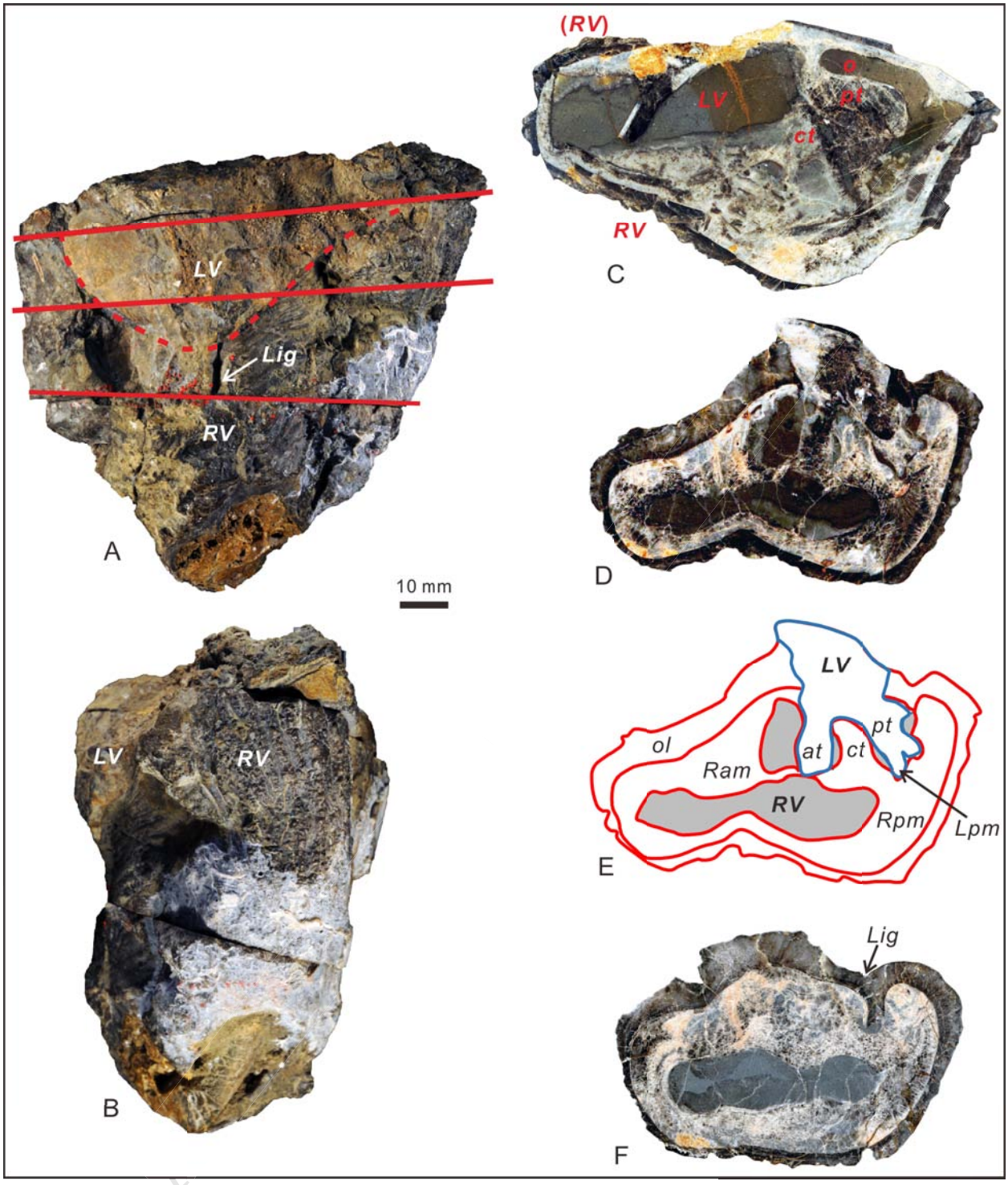

A
E79°
E81°
E83°
E85°
E87°
E89°
E91°
N34°
N32°
N30°
N28°
Rutog
Gar
Gegyai
Gerze
Qiangtang Block
Nyima
BNS
Qinghai
Baingoin
Coqen
Xainza
Namtso Lake
Lhasa Block
Zhongba
Low Himalaya
IYS
Sangzugang
Dazhuka
Lhasa
Xigaze
Tethyan Himalaya
Tingri
Gamba
High Himalaya
China
Tibet
B
Nyima
Dangqiong Lake
Wenbu
10 km
Langshan Formation
Lake
River
Fossil locality
National border
Provincial border
Provincial road
County road




ectomyophoral cavity
LV
Lam
Lpm
Ram
Rpm
RV
A
ectomyophoral cavity
LV
Lpm
Rpm
Ram
RV
B
LV
ectomyophoral cavity
Lam
Lpm
Ram
Rpm
RV
C
ectomyophoral cavity
LV
Lam
Lpm
Rpm
Ram
RV
D
ectomyophoral cavity
LV
Lam
Lpm
Ram
Rpm
RV
E
ectomyophoral cavity
LV
Lpm
Lam
Rpm
Ram
RV
F


LV
RV
A
10 mm
B
commissure
LV
d
c
b
a
RV
C
D




(RV)
LV
ct
RV
C
LV
Lig
RV
A
10 mm
D
LV
RV
B
LV
ol
pt
at
ct
Ram
RV
Rpm
Lpm
E
Lig
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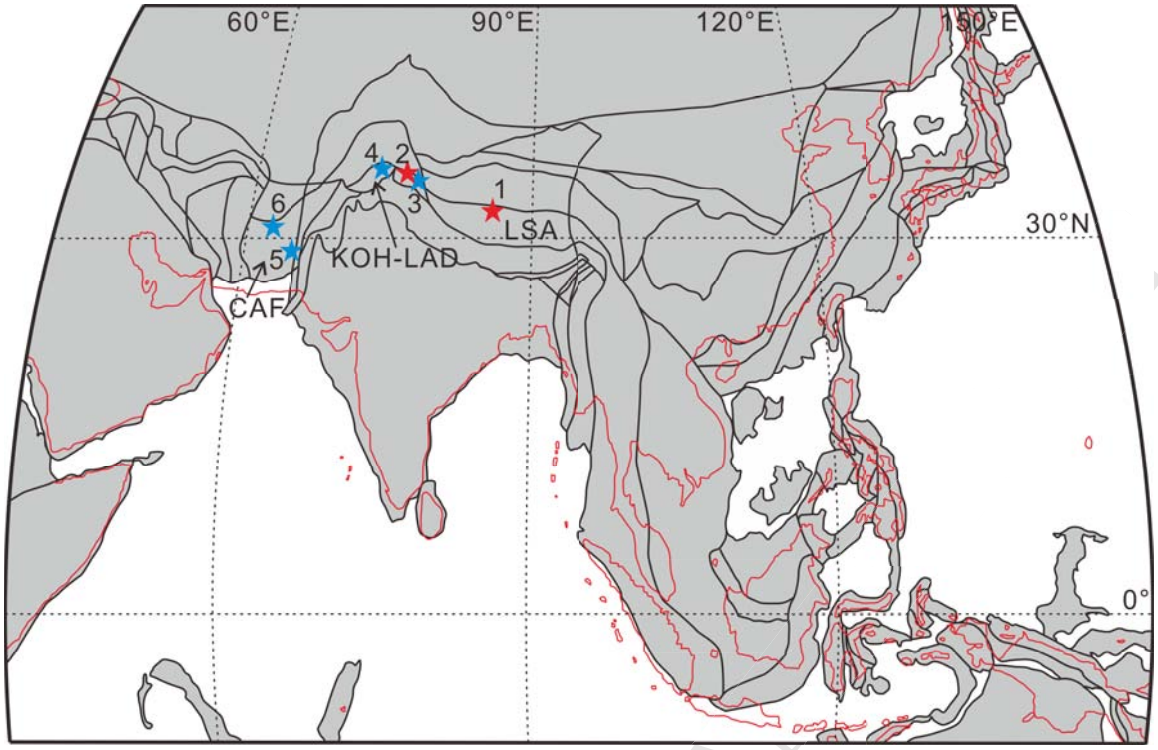

Highlights

1. A new polyconitid rudist *Shajia tibetica* gen. et sp. nov., likely late Aptian to Albian in age, is described from the Langshan Formation of Nyima County, Tibet.
2. *Shajia* is externally comparable with *Horiopleura haydeni* Douvillé, 1926, but differs in its possession of an inwardly inclined, instead of outwardly facing, posterior myophore in the right valve
3. A single specimen from Ladakh that was assigned to *Polyconites*? sp. by Masse and Fenerci-Masse (2017), is revised and transferred to *Shajia*.
4. The *Shajia tibetica* /*Auroradiolites biconvexus* rudist association can be considered a regional variant of the Yasin fauna.

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